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FURTHER STUDIES ON THE REPRODUCTIVE METHODS OF CERTAIN SPECIES OF COCCIDAE (HOMOPTERA)

By H. C. James, B.Sc., Ph.D., F.R.E.S.

(*Zoological Department, Cambridge.*)

With 1 Text-figure.

(Read 1st March, 1939.)

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(1) *Orthezia insignis* Doug.

Orthezia insignis is the commonest and most widely distributed species in the subfamily Ortheziinae, but despite its ubiquity and prevalence there appears to be only two records of males. Green (1904–9) when working in Ceylon observed them twice with an interval of four years between the records, and on each occasion they were stated to have occurred in enormous numbers.

In studying the reproductive habits of species in a group whose methods of reproduction vary so considerably as in the Coccidae the following possibilities—apart from any as yet undiscovered—have to be borne in mind.

(*a*) That the females of *O. insignis* might ordinarily be parthenogenetic, with an occasional production of males evoked in response to some stimulus which might include such factors as the kind of host, climatic conditions etc.

(*b*) Or that what appear to be the females of the species may really be functional hermaphrodites producing only hermaphrodites like themselves such as occurs in the Monophlebine *Icerya purchasi* Mask. but possibly without the occurrence of the casual males which *I. purchasi* is known to produce.

(*c*) Or that there are two races of *O. insignis* as in the case of certain Lecaniine scales, one obligatorily parthogenetic, producing only females, the other race exhibiting well-marked cytological differences and in which sexual reproduction occurs but in which the females may become facultatively parthenogenetic in the absence of males.

During the whole period of my study of *O. insignis*, extending over a period of three years and comprising, in addition to controlled experiments the results of which are shown in Table 1, frequent observations of it on a number of hosts in the Cambridge Botanic Gardens, not a single male in any stage was observed.

(2) The biology of reproduction in *Orthezia insignis*.

The period of time which elapses between the final moult and the first traces of the ovisac varies from six to twelve days (the average for seventy

TABLE 1.

The reproduction records of seventy females of *Orthezia insignis* Doug.

Family group	No. of ♀	Total progeny ♀♀	Duration of oviposition in days	Time of year oviposition took place	Average daily no. of progeny during period of oviposition
Families varying from 351–404	1	387	100	13.v.37–21.viii.37	3·870 +
	2	372	97	12.ix.37–17.xii.37	3·835
	3	404	114	14.v.37–4.ix.37	3·545 —
	4	378	112	10.viii.37–29.xi.37	3·375
	5	369	120	31.v.37–27.ix.37	3·075
Families varying from 301–350	6	348	92	19.vii.37–18.x.37	3·783 —
	7	312	92	21.v.37–21.viii.37	3·380 +
	8	327	98	15.v.37–20.viii.37	3·337 —
	9	301	96	14.iv.37–18.xii.37	3·135 +
	10	318	118	13.v.37–7.ix.37	2·356 —
Families varying from 251–300	11	273	72	10.iv.37–20.vi.37	3·792 —
	12	285	85	13.v.37–5.viii.37	3·353 —
	13	265	85	31.v.37–23.viii.37	3·118 —
	14	297	101	15.v.37–23.viii.37	2·941 —
	15	282	99	14.ix.37–21.xii.37	2·848 +
	16	258	93	19.v.37–27.ix.37	2·774 +
	17	251	95	8.iv.37–11.vii.37	2·642 +
	18	298	87	16.v.37–10.viii.37	2·425 +
	19	259	120	31.v.37–27.ix.37	2·158 +
Families varying from 201–250	20	241	78	13.ix.37–29.xi.37	3·090 —
	21	216	70	31.v.37–8.vii.37	3·086 —
	22	248	81	15.v.37–3.viii.37	3·062 —
	23	233	79	21.iv.37–8.vii.37	2·949 +
	24	210	73	20.v.37–31.vii.37	2·877 —
	25	204	71	26.v.37–4.viii.37	2·873 +
	26	203	71	10.viii.37–19.x.37	2·859 +
	27	213	75	16.v.37–29.vii.37	2·840
	28	214	78	7.v.37–23.vii.37	2·744 —
	29	216	83	13.viii.37–3.xi.37	2·624 +
	30	205	79	15.v.37–1.viii.37	2·595 —
	31	215	85	7.vi.37–30.viii.37	2·529 +
	32	220	91	15.v.37–13.viii.37	2·418 —
	33	207	86	21.iv.37–15.vii.37	2·407 —
	34	211	88	31.v.37–26.viii.37	2·398 —
	35	238	102	14.ix.37–24.xii.37	2·373 —
	36	206	90	19.vii.37–20.x.37	2·267 —
	37	209	94	31.v.37–1.ix.37	2·223 +
	38	205	120	6.vi.37–27.ix.37	1·708
Families varying from 151–300	39	193	65	20.v.37–23.vii.37	2·969 +
	40	197	68	20.v.37–26.vii.37	2·882 +
	41	200	70	21.iv.37–29.vi.37	2·857 +
	42	192	72	7.vi.37–17.viii.37	2·667 —
	43	186	70	15.v.37–23.vii.37	2·657 +
	44	192	74	31.v.37–22.viii.37	2·595 —
	45	198	77	13.viii.37–28.x.37	2·571 +
	46	193	77	8.vii.37–22.ix.37	2·505 —
	47	180	78	19.vii.37–4.x.37	2·308 —
	48	184	82	21.iv.37–11.vii.37	2·244 —
	49	195	90	13.ix.37–11.xii.37	2·167 —
	50	165	80	11.v.37–29.vii.37	2·0625
	51	162	99	13.v.37–19.viii.37	1·636 +

Family group	No. of ♀	Total progeny ♀♀	Duration of oviposition in days	Time of year oviposition took place	Average daily no. of progeny during period of oviposition
Families varying from 101–150	52	143	65	8.vii.37–10.ix.37	2·200
	53	112	55	7.iv.37–31.v.37	2·036 +
	54	116	59	15.v.37–12.vii.37	1·966 +
	55	104	57	19.vii.37–13.ix.37	1·824 +
	56	129	72	20.v.37–30.vii.37	1·792 —
	57	118	71	31.v.37–9.viii.37	1·662 —
	58	110	67	13.viii.37–18.x.37	1·642 —
	59	102	63	14.ix.37–15.xi.37	1·619 +
	60	119	76	22.v.37–5.viii.37	1·566 —
	61	122	81	17.ix.37–6.xii.37	1·506 +
	62	114	84	31.v.37–22.viii.37	1·357 +
	63	102	85	5.viii.37–28.x.37	1·200
Families varying from 51–100	64	96	45	15.v.37–28.vi.37	2·133 +
	65	79	38	20.v.37–26.vi.37	2·079 —
	66	98	63	15.v.37–16.vii.37	1·556 —
	67	99	68	7.iv.37–13.vi.37	1·456 —
	68	81	56	31.v.37–25.vi.37	1·446 +
	69	74	54	7.vi.37–30.vii.37	1·370 +
	70	73	59	26.v.37–23.vii.37	1·237 +
		14526	5690		

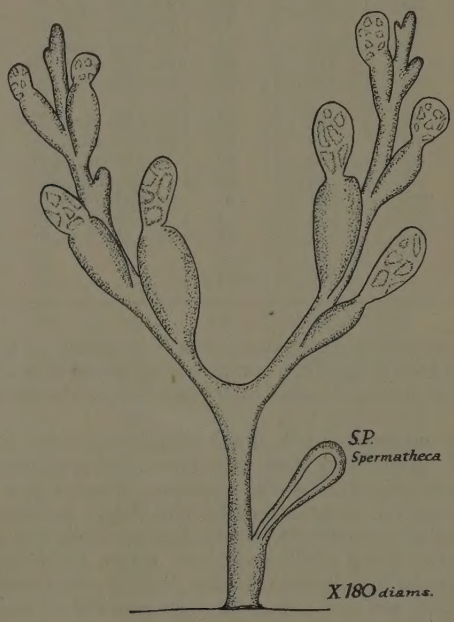
females in the controlled experiments was 8·30 days). The growth of the ovisac covers the genital aperture, completely enclosing it so that if copulation does occur in this species it must take place before the development of the ovisac begins.

The ovisac or marsupium is a fluted slightly upcurved structure of hard white wax about 1¼ inch long when fully grown and is attached to the hinder end of the female over the genital aperture. Despite this relatively long appendage, however, the female remains completely mobile throughout life. The ovisac takes from fourteen to twenty days to attain full size (the average for seventy females being 17·74 days) but before the ovisac is completed oviposition begins and the eggs are extruded into the ovisac swathed in a mass of waxy threads which are secreted as the eggs pass out of the vagina. There may be upwards of fifty maturing ova arranged in neat rows within the ovisac and varying in appearance from water-white newly oviposited eggs to greenish-brown ones containing almost fully formed embryos. Embryonic development is both begun and completed within the ovisac, since sections of ovipositing females reveal that not even the first cleavage division is effected before oviposition. After eclosion the first-born nymphs break their way out at the distal end of the ovisac and thereafter the remaining progeny pass through the aperture thus made. Oviposition is a somewhat lengthy process in this species and is carried on without any well-marked intermission until the female is presumably exhausted as death speedily follows its cessation. The period of oviposition in the controlled experiments varied from a minimum of thirty-eight to a maximum of one hundred and twenty days with an average for seventy females of 65·57 + days.

The daily number of progeny emerging from the ovisac varies from one to four and is greater in females of high fecundity than in those of low, since in

general the total number of eggs oviposited does not vary directly with the length of the period of oviposition.

Mature females of *O. insignis* vary little in size but the total progeny from individual females in Table 1 varied from as few as thirty-eight to as many as four hundred and four. The comparative slow rate of oviposition makes it possible to measure with great exactitude the fecundity of each female, and the wide variation in the size of families is almost entirely due to variations in fecundity of individual females. The table on pp. 570–571 gives the total progeny, length of the period of oviposition and average daily number of progeny from seventy females.



The average number of progeny per female = 218·86 —.

Previous published records of the reproductive capacity of this species are much too low. Despite the complete absence of records of males in the above table the total progeny from 70 females bred under controlled conditions is double that reported by previous workers.

(3) The female genital organs of *O. insignis*.

The ovaries of *O. insignis* (fig.) conform fairly closely to the usual Coccidoid type, consisting of two hollow tubes which unite posteriorly to form a rather long vagina opening to the exterior.

The oocytes with their attendant nurse cells develop on the walls of the oviduct in sessile ovarioles. In spite of the absence of males, or at any rate their very rare occurrence, a large spermathecal-like organ (SP in figure) is present. Apart from the apparent lack of the necessity for such a well-

developed structure in this species there is some doubt in other groups of the COCCIDAE as to whether such organs have the functions ordinarily attributed to spermathecae in the Insecta. For instance, a somewhat similar structure opens into the vagina in PSEUDOCOCCINAE, but its function seems to be doubtful since many ova are certainly fertilised *in situ* in the ovarioles and masses of sperms are normally present in the vagina of breeding females.

The external appearance of the ovaries showed none of the abnormalities associated with functional hermaphroditism as described by Hughes-Schrader (1925) in *Icerya purchasi* (MONOPHLEBINAE) nor did sections of the ovaries disclose the presence of spermatogenous tissue, and it is clear that the unisexual nature of the progeny of *O. insignis* is due not to hermaphroditism but to diploid parthenogenesis.

(4) The sex ratio of *Pseudococcus nipae* (Maskell).

Pseudococcus nipae is a relatively small species commonly occurring on palms, bananas, and kindred plants and has a wide distribution in tropical and subtropical regions and in greenhouses in temperate zones. As its relatively small size might lead one to expect, the average fecundity of the females is considerably below that of larger species, e.g., *P. citri* (Risso), *P. gahani*, and *P. longispinus* (Targ.).

Although very little ovisac is produced, *P. nipae* is oviparous, and the species was ascertained to be strictly zygogenetic; knowledge concerning the presence or absence of parthogenesis is an essential pre-requisite for the study of sex ratios particularly in a family like the COCCIDAE in which facultative parthenogenesis is known to occur. In species where facultative parthenogenesis is possible, delay in fertilisation may result in the production of both zygogenetic and parthenogenetic progeny with a consequent derangement of the sex ratios.

The species of host-plant selected for the breeding of *P. nipae* was the date palm *Phoenix silvestris*, which proved very suitable on account of its hardiness and longevity. Single females were isolated on potted plants and were enclosed under cellophane-capped lamp glasses as already described for previous work of this nature. The range of temperature during the experiment varied from 24·44° C. to 28·28° C. with a mean for the period of 25·63° C. The plants and insects were maintained in saturated air throughout the experiment.

I wish to thank Mr. H. Morrison of the U.S. Bureau of Entomology for kindly confirming the identity of the species.

The body of breeding data on pp. 574–575 shows conclusively that in the species *P. nipae* there is a marked disparity in the number of the sexes, since considerably more than twice as many females as males are produced. With the exception of a few aberrant ratios which may be due to one or more undetermined causes such as the action of a gene or genes disturbing the action of the heterogametic mechanism or to an undetected differential sex mortality most of the family ratios lie in the region of 20 to 50 and there is no doubt that this is the zone in this species wherein such ratios normally fall.

That some form of XY mechanism plays a major part in sex determination in *Pseudococcus* is evident from the fact that though no individual chromosomes can be recognised as being specially concerned with sex constant, qualitative differences can be detected between the two sets of chromosomes going to opposite poles in the reduction division of the male. Moreover, it may be mentioned that Thomsen (1927) has shown in a neighbouring group of the

TABLE 2.

A series of 66 family sex ratios of *Pseudococcus nipae* Maskell.

Family group	No. of ♀♀	Total progeny	♂♂	♀♀	Per 100
Families varying from 151–200	1	196	61	135	45·11 +
	2	175	48	127	37·80 —
	3	169	39	130	30·00
	4	174	38	136	27·93 —
	5	176	34	142	23·94 +
Families varying from 101–150	6	101	56	45	124·44 +
	7	118	41	77	53·25 —
	8	108	35	73	47·95 —
	9	118	34	84	40·48 —
	10	135	38	97	39·18 —
	11	121	32	89	35·96 —
	12	135	34	101	33·66 +
	13	139	32	107	29·91 —
	14	101	21	80	26·25
	15	140	29	111	26·13 —
	16	112	22	90	24·44 +
	17	105	17	88	19·32 —
Families varying from 51–100	18	59	28	31	90·32 +
	19	63	25	28	65·79 —
	20	63	22	41	53·66 —
	21	71	24	47	51·06 +
	22	61	20	41	48·78 +
	23	73	23	50	46·00
	24	64	20	44	45·45 +
	25	68	21	47	44·68 +
	26	69	21	48	43·75
	27	57	17	40	42·50
	28	86	24	62	38·71 —
	29	95	26	69	37·68 +
	30	69	18	51	35·29 +
	31	96	24	72	33·33 +
	32	99	24	75	32·00
	33	62	15	47	31·91 +
	34	59	14	45	31·11 +
	35	72	17	55	30·91 —
	36	79	17	62	27·42 —
	37	84	18	66	27·27 +
	38	96	19	77	24·67 +
	39	91	14	77	18·18 +
	40	96	13	83	15·66 +
	41	68	6	62	9·68 —
	42	31	23	8	287·50
	43	37	16	21	76·19 +
	44	42	18	24	75·00
	45	19	7	12	58·33 +
	46	41	15	26	57·69 +
	47	33	12	21	57·14 +
	48	22	8	14	57·14 +
	49	46	16	30	53·33 +
	50	30	10	20	50·00
	51	48	15	33	45·45 +
	52	23	7	16	43·75

Family group	No. of ♀♀	Total progeny	♂♂	♀♀	Per 100
Families varying from 51–100	53	50	15	35	42·86
	54	28	8	20	40·00
	55	18	5	13	38·46 +
	56	37	10	27	37·04 —
	57	30	8	22	36·36 +
	58	39	10	29	34·48 +
	59	48	12	36	33·33 +
	60	38	9	29	31·03 +
	61	49	11	38	28·95 —
	62	45	10	35	28·57 +
	63	49	10	39	25·64 +
Families varying from 0–50	64	45	9	36	25·00
	65	28	5	23	21·74 —
	66	22	2	20	10·00
		5021	1352	3669	2886·54

Specific sex ratio = 43·70 ± 4·37
Average size of family per ♀ = $\frac{5021}{66}$ = 76·08 —

Lecaniinae that certain species in which facultative diploid parthenogenesis may occur fertilised eggs produce bisexual progeny thus indicating that the male is heterogametic for sex.

It is certain that in *P. nipae* as in the five other Pseudococcine species examined in a previous paper (James, 1937) that the heteropycnotic and the loose groups of chromosomes into which the diploid number of ten is equally divided in the male and which separate from each other at meiosis produce fully formed externally indistinguishable sperms, the product of each reduction division being a double spermatid of two externally similar spermatozoa.

Based on the fact that the spindle fibres attached to the loose group in the reduction division are formed later and in an irregular manner and that the meiotic stages of the male germ cells of *Pseudococcus* bear considerable resemblance to the same phases in the haploid males of various Hymenoptera, Schrader considers the possibility that the loose group may lack certain properties which would make them equivalent to the massed group. He concluded with the statement " whether this lack is indicative of a loss and whether this loose group is on its way to disappearance must be left to further investigation. If either of these surmises is correct the origin of haploid males is near solution. In this connection it may not be amiss to point out that at least one species with haploid males occurs among the Homoptera (*Trialeurodes* Schrader 1920) the order in which *Pseudococcus* is a member."

Hence the study of the sex ratios of *P. nipae* and other species of *Pseudococcus* revealing a series of unbalanced ratios in which the female sex shows varying degrees of predominance suggest that the nucleus of the male-producing gamete is derived from the loose group of chromosomes and that the evolution of haploid males is taking place in *Pseudococcus*.

(5) Reproduction in *Saissetia nigra* (Nietner).

Saissetia nigra is a very prolific and polyphagous species of world-wide distribution. It was found growing on a considerable diversity of host species

in the Cambridge Botanic Gardens, of which the following is a list of the commoner ones, *Asystasia bella*, *Pavonia spinifex*, Ferns, *Ficus religiosa*, *Clusia flava*, *Aristolochia labiosa*, *A. kewensis*, *A. braziliensis*, *Musa martini*, *Philodendron erubescens*, *Phoenix silvestris*, *Anthurium bakeri*, *Spathyphyllum cochlearispathum*, *Cedrela odorata*, *Nepenthes williamsi*, *Solandra Hertwigii*.

Although the species occurred in great numbers on certain hosts and observations were made during a period of two years, only the female sex was found. This provided almost conclusive evidence that kind of host-plant has no noticeable influence on the production of males.

Similarly, experiments under controlled conditions in which the female was bred on the date palm, *Phoenix silvestris*, all the progeny, numbering 13,688, were females. The reproductive capacity of the thirty-seven females used in these experiments varied from 4 to 637 with an average family per female of 369·95 —. The method of oviposition did not enable its duration to be observed with precision, but as the sex of the progeny became evident they were counted and removed. Since Green (1904–9) has described the male of this species from Ceylon it appears probable that in this species, as in certain other Lecaniines, there are both obligatorily and facultatively parthenogenetic races. If this is the case it seems certain that I have been working solely with the race in which parthenogenesis is obligatory and in which the progeny consists entirely of females.

TABLE 3.

The progeny from 37 ♀♀ of *Saissetia nigra*.

Family Group	No. of ♀	Total progeny	Family Group	No. of ♀	Total progeny
601–650	1	637	351–400	20	390
551–600	2	580		21	377
	3	561		22	368
501–550	4	545		23	366
	5	542		24	364
	6	519		25	355
	7	514	301–350	26	349
	8	511		27	318
451–500	9	495		28	313
	10	485		29	308
	11	470		30	302
	12	459	251–300	31	290
	13	457		32	261
	14	455	201–250	33	209
	15	453	151–200	34	142
	16	452		35	117
401–45	17	446	51–100	36	65
	18	432	0–50	37	4
	19	414			
				Total progeny	14325

Average progeny per ♀ = 369·95 —

SUMMARY.

(1) In controlled experiments with *Orthezia insignis* on a species of *Coleus* families consisting of females only were obtained. The male of the species was never found. Dissections and histological examination of the ovaries failed to

disclose any indication of hermaphroditism and it is certain that the unisexuality of the progeny is the result of diploid parthenogenesis.

(2) The fecundity of *O. insignis* is much higher than previously published accounts indicated. The largest family obtained from among 70 females was 404 ♀♀ with an average family per female of 218·86 — ♀♀. The mode of oviposition in this species enabled the length of the egg-laying period to be measured with great preciseness. It varied from 38 to 120 days with an average per female of 65·57 + eggs from 70 females.

(3) *Pseudococcus nipae* was found to be oviparous and reproduction is entirely zygogenetic. The family sex ratios of 66 females reared on the date palm *Phoenix silvestris* varied from 10 ♂♂ per 100 ♀♀ to 287·50 ♂♂ per 100 ♀♀ but the zone in which the family ratios of this species usually fall is between 20 and 50 ♂♂ per 100 ♀♀. The specific sex ratio worked out at 43·70 ± 4·37 ♂♂ per 100 ♀♀. The fecundity of the species is low for the PSEUDOCOCCINAE and averaged 76·08 — per female.

(4) The markedly unbalanced nature of the specific sex ratio of *P. nipae* provides further evidence that the male-producing sperm in *Pseudococcus*, though produced in numbers equal to those of the females, is functionally much less efficient. Evidence is also adduced that the evolution of haploid males is taking place in *Pseudococcus*.

(5) Controlled experiments with breeding females of *Saissetia nigra* resulted in progeny of only one sex. 37 ♀♀ produced 13,688 individuals, all of which were ♀♀. In addition, close observation of the species on its common hosts failed to disclose a male. In view of the description of the male from other parts of the world it is probable the material studied represents an obligatorily parthenogenetic race of the species.

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